Available online at www.sciencedirect.com
ScienceDirect
Forest Ecology and Management 233 (2006) 338–343
Forest Ecology and Management
www.elsevier.com/locate/foreco

Growth in pure and mixed plantations of tree species used in reforesting rural areas of the humid region of Costa Rica, Central America

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Abstract

This paper compares productivity of native tree species plantations, in monoculture and mixtures, at La Selva Biological Station in the Caribbean lowlands of Costa Rica. In monocultures, *Jacaranda copaia*, *Vochysia guatemalensis*, and *Vochysia ferruginea* were the most productive of 10 species compared. However, *J. copaia* and *V. guatemalensis* grew significantly faster in mixtures than in monocultures. A mixture of *J. copaia*, *V. guatemalensis*, and *Calophyllum brasiliense* produced 21% more merchantable volume than a monoculture of *J. copaia*, which grew the fastest of the three species. Mixed plantations of *Dipteryx panamensis*, *Virola koschnyi*, and *Terminalia amazonia* had productivity rates similar to monocultures of the fastest growing of these species (*Virola koschnyi*). The productivity of mixed plantations of *V. ferruginea*, *Hyeronima alchorneoides*, *Genipa americana*, and *Balizia elegans* was intermediate from the respective species' productivities in monocultures. Cultivating tree species in mixtures affected species' growth forms and ability to persist on the site.

Keywords: *Vochysia ferruginea*; *Vochysia guatemalensi*; *Hieronyma alchorneoides*; *Genipa americana*; *Balizia elegans*; *Jacaranda copaia*; Mixed-species

1. Introduction

In Costa Rica there have been government incentives for establishing and maintaining native tree species plantations since the 1990s (Piotto et al., 2003a). These reforestation projects have been established by owners of small and medium-sized farms. These farmers often have no training or experience in intensive tree plantation management (Haggar et al., 1998). Little knowledge exists about the long-term performance of native tree species under varying management regimes, including the use of pure or mixed-species plantation designs. In particular, productivity levels of neotropical native tree species in plantations are by and large unknown (Montagnini et al., 1995; Piotto et al., 2003a). Such information is necessary to reduce investment risks for farmers.

The present study describes results from a long-term research project investigating native tree species performance on degraded lands in the lowland, humid Caribbean region of Costa Rica, Central America. The study plots are in pure and mixed-species plantations located on abandoned pasturelands at La Guaria Annex of La Selva Biological Station. The overall goals of the research included evaluations of tree productivity as well as environmental services provided by the plantations. Results of previous research comparing the same experimental pure and mixed-species plantations at La Selva have shown that mixed plantations grow well, with productivities either similar or greater than the same species grown in monocultures (Piotto et al., 2003a,b; Alice et al., 2004; Petit and Montagnini, 2004). As a consequence, mixed plantations also accumulate above-ground biomass and sequester carbon at rates comparable to monocultures (Montagnini and Porras, 1998; Stanley and Montagnini, 1999). These same mixed plantations have also been shown to contribute to recovery of soil fertility of abandoned pasturelands (Montagnini and Porras, 1998). Results of previous research also showed that these plantations facilitate regeneration of native woody species under their canopies thus serving to restore biodiversity in degraded lands (Carnevale and Montagnini, 2002; Cusack and Montagnini, 2004; Montagnini et al., 2005).

Growth equations based on these experimental plantations have been previously constructed for each of the 10 species growing in the plantations. Rotation ages and the merchantable volume produced after a single rotation were calculated for each of the species using a maximum sustained yield approach (Petit and Montagnini, 2004). In the present article, the growth

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0378-1127/$ – see front matter
doi:10.1016/j.foreco.2006.05.030

Table 1
Characteristics of tree species grown in experimental plantations at La Selva Biological Station in the Caribbean lowlands of Costa Rica

Species name	Common name	Family	Native range	Growth, habitat
Plantation 1				
Vochysia guatemalensis Donn. Sm.	Chancho, mayo	Vochysiaceae	Mexico to Panama	Upper canopy, early-mid successional. Fast growth
Callophyllum brasiliense Cambess.	Cedro Maria	Clusiaceae	Mexico to South America and the Antilles	Canopy tree. Moderately shade –tolerant. Slower growth
Jacaranda copaia (Aubl) D. Don	Jacaranda	Bignoniaceae	Guatemala to Brazil	Upper canopy, early successional. Fast growth
Plantation 2				
Terminalia amazonia (J.F.Gmel.) Exell	Amarillon, roble coral	Combretaceae	Mexico to South America and the Antilles	Canopy tree. Heliophyllous. Moderately fast growth
Virola koschnyi Warb	Fruta dorada	Myristicaceae	Belize to Panama and Ecuador	Canopy tree, mid-successional. Slower growth
Dipteryx panamensis (Pittier)Record & Mell	Almendro	Fabaceae—Papilionoideae	Nicaragua to Colombia	Canopy tree, late successional. Slower growth
Plantation 3				
Hyeronima alchorneoides Fr. Allemao	Pilon	Euphorbiaceae	Belize to the Amazon	Canopy tree, early – mid successional. Moderately fast growth
Vochysia ferruginea Mart.	Botarrama	Vochysiacea	Nicaragua to Peru and Brazil	Heliophyllous tree, rapid growth. Found in secondary forests
Balizia elegans (Ducke) Barnaby and Grimes	Ajillo	Fabaceae—Mimosoideae	Tropical America	Mid- to late successional. Slower growth
Genipa americana L.	Genipa	Rubiaceae	Tropical America	Late successional. Slower growth

Source: Holdridge and Poveda (1975), Jiménez and Poveda (1997) and Jiménez-Madrigal et al. (2002).

of these species in mixed plantations and monocultures are compared in order to make recommendations to landowners. The species studied are those most utilized by local farmers in the region (Piotto et al., 2003b), and most of them have broad distribution throughout the Neotropics as shown in Table 1.

2. Materials and methods

2.1. Study site description

Experiments were established on abandoned pasture at La Selva Biological Station, Costa Rica—humid tropical lowlands (10°26′N, 86°59′W, 50 m mean altitude, 24 °C mean annual temperature, 4000 mm mean annual rainfall). Soils are Fluventic Dystropepts derived from volcanic alluvium; they are deep, well-drained, stone-free, acidic (pH in water < 5.0), with low or medium amounts of organic matter (2.5–4.5%), cation exchange capacity 10–14 cmol kg^{-1}, 10–15% base saturation, and moderately heavy texture (50–60% sand, 5–15% silt, and 25–45% clay) (Sancho and Mata, 1987). According to standards set by the Costa Rican Ministry of Agriculture, fertility levels of the site, especially of cations and P, were too low for conventional agriculture as practiced in the region (Montagnini and Porras, 1998). This is relevant because the overall objectives of the research were to find alternative land uses for recovery of degraded pasturelands in the region.

The area was cleared in the mid-1950s and grazed until 1981, a land-use pattern common in the region. The area is on flat, uniform terrain (<1 m average difference between lowest and highest points). At the time of clearing for the plantations, the area was covered with shrubs and early successional trees interspersed with patches of grass and ferns. In comparing soil chemical characteristics before planting, results showed that there were no significant differences among blocks within each plantation, as well as between the three plantations (Montagnini et al., 1993).

The selection criteria of the tree species in the study were: preliminary data on growth rate, farmer preference, potential impacts on soil fertility, general characteristics of nutrient recycling, and availability of plant stock (Montagnini et al., 1993, 1995). For the design of each of the three plantations, four tree species were initially selected, including both fast and slow-growing species. The combination of species was chosen to ensure different branching patterns, size, and crown shape (Montagnini et al., 1995). In each mixed-species plot, at least one legume, one relatively fast, and one relatively slow-growing species were planted. Within each mixed-tree plot, trees of the four species were planted alternating two species per row. The sequential order of the species within rows was systematically reversed every other row. In that manner, each column contained the four species of the mixture in a sequence. Thus, each row has all four species, as follows:

1	3	2	4
2	4	1	3
1	3	2	4
2	4	1	3

Plantations were set in randomized blocks, with four replicates and six treatments: four pure plantation plots of each species, a mixed-species plot (with the four species), and a

Table 2
Growth equations for pure and mixed plantations in Plantation 1

Species	Growth equation[a]	R^2-value
Vochysia guatemalensis	$V = -1.2983t^3 + 16.562t^2 - 11.441t,\ ^{\forall}t \mid t < 8.3$	0.967
	$V = -0.4939t^3 + 13.437t^2 - 55.039t,\ ^{\forall}t \mid t > 8.3$	0.738
Calophyllum brasiliense	$V = -0.0711t^3 + 2.6340t^2 - 5.5421t$	0.950
Jacaranda copaia	$V = -0.1462t^3 - 0.0343t^2 + 52.615t$	0.940
Mixture	$V = -0.7977t^3 + 13.569t^2 - 1.9627t$	0.965

Source: Petit and Montagnini (2004).
[a] As seen as variables in the above equations, V is estimated volume of timber produced in m^3/ha, and t is time in years.

fallow (natural forest regrowth) plot where no tree planting was done. Each plot measured 32 m × 32 m with an initial tree density of 2 m × 2 m, thinned to 4 m × 4 m 6 years after establishment. No further management interventions were done in the plantations after the thinnings. Each plantation is about 2.5 ha.

The plantations used in this research were established in 1991–1992. Plantations were 10–11 years old at the time the present research took place. There are three plantations that originally contained four species each. Two species have suffered severe mortality due to pests and diseases: *Stryphnodendron mycrostachyum* in Plantation 1 (anthracnosis at 3 years) and *Paraserianthes falcataria* in Plantation 2 (attack by root gophers at 5–6 years) (Montagnini et al., 1995; Montagnini and Porras, 1998). Thus, for the present research there were 10 species for consideration. The 10 species were as follows: *Plantation 1—Calophyllum brasiliense* Cambess, *Vochysia guatemalensis* Donn.Sm., and *Jacaranda copaia* (Aubl.) D.Don.; *Plantation 2—Dipteryx panamensis* (Pittier) Record & Mell, *Virola koschnyi* Warb., and *Terminalia amazonia* (J.F. Gmel.) Exell.; *Plantation 3—V. ferruginea* Mart., *Hyeronima alchorneoides* Allemao, *Genipa americana* L., and *Balizia elegans* (Ducke) Barneby & Grimes (Table 1).

2.2. Experimental design for measurements

Subplots were laid out in each of the four plots of each species in pure and in mixed designs. For consistency, the subplots were laid out in the same manner as in previous measurements (Piotto et al., 2003a; Alice et al., 2004). Eight meters on each side of the experimental plots were excluded as buffers to eliminate potential border effects (Rustagi, 1993). All of the remaining trees in the plot were measured. Each tree's diameter at breast height (cm) and total height (m) were measured. The mean diameter at breast height and total height were calculated and used to represent average diameter at breast height and total height for each plot. The area of each subplot, tree basal area and the volume of merchantable wood standing in the subplot were calculated (Hairiah et al., 2001; Petit and Montagnini, 2004). The volumes were calculated using the formula $V = \alpha \times B_{dbh} \times H$, where α is the stem form factor, B_{dbh} the basal area, and H is the total height. The value of α was set to 0.5 (Ugalde, 2000). In separate research, form factors are being calculated for each of the species based on field measurements taken at time of thinning. The form factors calculated for the species of this research range between 0.5 and 0.58, therefore it is assumed that using 0.5 is close enough for the purposes of the present article (Petit and Montagnini, unpublished data).

Previously published growth equations (Table 2; Petit and Montagnini, 2004) were used to estimate mean annual increments (MAIs) for the plots in Plantation 1. The age at which MAI was maximized, was identified to the month. This age was deemed to be the optimal rotation age for these species and/or mixtures under these conditions (Newman, 2002; Smith et al., 1996). The mixtures were assumed to be harvested in entirety in one entry, regardless of individual species growth. Additionally, the volume of wood produced at this age was computed for each species/mixture by entering this age into the extrapolative growth equations produced earlier (Knoebel et al., 1986). This total volume was converted to merchantable volume (amount of timber in logs to be removed from the stand) by subtracting 15% from the total wood volume (Vanclay, 1996; Wright and Alder, 2000). These calculated rotation ages and simulated volumes were used to compare productivities between pure and mixed plantations (Burkhart and Than, 1992). Mean annual increments were estimated for each species and mixture.

Growth of the species in Plantations 2 and 3 had not begun to slow by 10 years of age; consequently, reliable growth equations could not be constructed. Thus, the rotation ages for species and mixtures in Plantations 2 and 3 were assumed to be the most recent measure (age 10 years), and their yields were assumed to be their standing volumes on that date. Comparisons between species and mixtures were made amongst the stands in Plantation 1; separate comparisons were made amongst stands in Plantations 2 and 3. In the mixtures, no differentiation amongst the types of wood was considered in the comparisons.

2.2.1. Comparisons of species growth in pure and mixed-species plantations

The growth of trees in mixed plots was compared to the growth of the trees of the same species in the monocultures in Plantations 1–3 to determine whether trees of particular species grow larger in monocultures or mixtures. Unpaired, two-tailed t-tests were performed to test for significant differences between the average volumes of wood present in trees of the same species under the two growing regimes (Whyte and Woollons, 1990).

Table 3
General growth and productivity statistics of pure and mixed, native species plantations at La Selva, Costa Rica

Species	Age (years)	Density (trees/ha)	Diameter at breast height (cm)	Total height (m)	Basal area (m^2/ha)	Merchantable volume (m^3/ha)	MAI volume (m^3/ha)	MAI DBH (cm /year)	MAI height (m/year)
Plantation 1									
V. guatemalensis	11	571 (101)a	25.2 (0.7)a	26.0 (0.8)a	27.9 (3.7)a	307 (36)a	27.9 (3.3)a	2.3 (0.1)a	2.4 (0.1)a
C. brasiliense	11	872 (324)a	18.0 (0.3)b	16.9 (0.2)c	21.8 (7.6)a	158 (56)a	14.4 (5.1)a	1.6 (0.0)b	1.5 (0.0)c
J. copaia	11	648 (54)a	22.5 (0.7)a	23.2 (1.2)b	25.7 (2.0)a	252 (19)a	22.9 (1.7)a	2.0 (0.1)a	2.1 (0.1)ab
Mixture	11	610 (77)a	24.7 (0.7)a	23.2 (0.5)b	28.8 (3.0)a	283 (28)a	25.7 (2.5)a	2.2 (0.1)a	2.1 (0.0)b
Plantation 2									
T. amazonia	11	494 (45)b	23.0 (1.2)a	22.7 (0.9)a	20.3 (1.7)b	197 (20)b	17.9 (1.8)b	2.1 (0.1)a	2.1 (0.1)a
V. koschnyi	11	756 (60)a	22.8 (1.1)a	22.3 (0.5)a	30.6 (1.8)a	290 (18)a	26.4 (1.6)a	2.1 (0.1)a	2.0 (0.0)a
D. panamensis	11	679 (95)a	15.1 (0.4)b	19.3 (0.5)b	11.9 (1.4)c	98 (11)c	8.9 (1.0)c	1.4 (0.0)c	1.8 (0.0)c
Mixture	11	571 (30)b	21.4 (1.3)a	21.2 (0.5)ab	20.5 (1.5)b	184 (11)b	16.7 (1.0)b	1.9 (0.1)b	1.9 (0.0)b
Plantation 3									
H. alchornoeides	10	694 (41)ab	16.9 (0.4)b	17.7 (0.8)a	15.5 (0.3)b	117 (7)b	11.7 (0.7)b	1.7 (0.0)c	1.8 (0.1)a
V. ferruginea	10	610 (46)ab	21.9 (1.0)a	19.8 (0.7)a	22.7 (1.3)a	192 (17)a	19.2 (1.7)a	2.2 (0.1)a	2.0 (0.1)a
B. elegans	10	640 (53)ab	18.2 (0.4)b	19.3 (0.8)a	16.9 (2.0)ab	139 (19)ab	13.9 (1.9)ab	1.8 (0.0)b	1.9 (0.1)a
G. americana	10	432 (103)c	13.3 (1.4)c	12.7 (0.8)b	6.1 (1.7)c	35 (11)c	3.5 (1.1)c	1.3 (0.1)d	1.3 (0.1)b
Mixture	10	710 (33)a	18.1 (0.5)b	18.2 (0.7)a	18.4 (1.5)ab	141 (9)ab	14.1 (0.9)ab	1.8 (0.0)b	1.8 (0.1)a

Values are means and standards errors (in parenthesis), for four replicate plots per treatment.
MAI (mean annual increments) are calculated from current ages, not rotation ages.
Significant differences in mean values between the treatments in each column are indicated by different lower-case letters (a–c) ($P < 0.05$).

3. Results

3.1. Growth and productivity attributes of pure and mixed plantations

Growth and productivity statistics of Plantations 1–3 appear in Table 3. Tree density remained fairly consistent amongst the plantations with one notable exception. Heavy mortality in *G. americana* plots caused a significant decrease in stand density (approximately 30–40%.) *C. brasiliense* and *D. panamensis* had significantly smaller diameters than other species in their plantations. Two of the species in Plantation 3 significantly varied in diameter from the others: *V. ferruginea* had a larger diameter and *G. americana* had a smaller diameter than the other species or mixture. While only *D. panamensis* and *G. americana* varied from their counterparts in height, all three species in Plantation 1 were stratified in height. While basal area remained consistent in Plantation 1, *V. koschnyi* and *V. ferruginea* plots had a significantly higher basal area than other monocultures or mixtures in Plantations 2 and 3.

3.2. Expected volume yields of pure and mixed plantations

For Plantation 1, the expected yields after one rotation for monocultures and mixed-species plantations as calculated from their respective growth equations, suggest that a monoculture of *V. guatemalensis* will produce 41–64% more merchantable wood at the end of a single rotation than monocultures of equal age and spacing of either *C. brasiliense* or *J. copaia* (Table 4). Furthermore, the pure *V. guatemalensis* plots are expected to yield 3% more volume after a single rotation than the three-species mixtures. However, the rotation length of the pure *V. guatemalensis* plots is 63% longer than the rotation length of the mixtures. The mixture in Plantation 1 yields 17% more merchantable wood per annum than the fastest growing pure species in Plantation 1.

Calculation of yields of tree species in Plantations 2 and 3 revealed that in Plantation 2, the mixtures produced more merchantable wood (88% more) in 11 years than the monocultures of *D. panamensis* (Table 3). On the other hand, the *T. amazonia* monocultures and the *V. koschnyi* monocultures yielded 7–58% more wood after 11 years than the mixtures. However, the *T. amazonia* monocultures were not significantly different in volume from the mixed-species plots.

In Plantation 3, the four-species mixtures produced on an average 27% less merchantable wood than monocultures of *V. ferruginea* after 10 years (Table 3). The yields of the pure *B. elegans* plots were variable, while little variance existed among the yields of the mixtures. Consequently, no statistically significant difference existed between the yields from the *B. elegans* monocultures and the mixtures. However, the *V. ferruginea* monocultures produced significantly more wood than the mixtures, and plot yields varied no more than average.

Table 4
Productivity in monocultures and mixtures in Plantation 1, estimated from growth equations

Species	Rot. age (years)	M. Vol. at harvest (m^3/ha)	Mean annual increment (m^3/ha/year)
V. guatemalensis—pure	13.5	417	30.9
C. brasiliense—pure	18.5	296	16.0
J. copaia—pure	6.5	255	39.2
Mixed species	8.5	403	47.4

Rot. age, rotation age. M. Vol. at harvest, merchantable volume yielded after one rotation.

Table 5
Differences in species growth amongst individuals in pure and mixed plots determined by way of an unpaired *t*-test

Species	V_{Pure} (m^3)	V_{Mixed} (m^3)	*P*	Best alternative
C. brasiliense	0.22	0.05	<0.0001	Pure
J. copaia	0.47	0.82	<0.0001	Mixed
V. guatemalensis	0.63	0.94	0.0003	Mixed
D. panamensis	0.19	0.18	0.414	–
V. koschnyi	0.46	0.37	0.042	Pure
T. amazonia	0.49	0.80	0.0002	Mixed
V. ferruginea	0.39	0.32	0.048	Pure
H. alchorneoides	0.21	0.27	0.026	Mixed
G. americana	0.10	0.08	0.222	–
B. elegans	0.29	0.24	0.167	–

The monocultures of *D. panamensis* and *G. americana* yielded relatively little merchantable wood after 10 years of growth (47–75% less than the mixtures). Several of the *G.* americana monocultures suffered heavy mortality (30–35%) during the 10th year.

3.3. Species growth in pure and mixed-species plantations

For 7 of the 10 tree species, individual trees were more productive depending on whether they grew in monocultures or multiple-species stands (Table 5). Volumes of *D. panamensis*, *G. americana*, and *B. elegans* trees did not significantly differ depending on whether they were grown in monocultures or mixtures. Though individual trees from these three species appear to be more productive in monocultures than in mixtures, the large degree of variation in their tree sizes within either plantation type negated any statistically significant differences. The canopies of pure plots of any these species had conspicuously differentiated.

Individual *C. brasiliense*, *V. koschnyi*, *V. ferruginea*, and *H. alchorneoides* trees produced more volume in monocultures than in mixtures. Individual *J. copaia*, *V. guatemalensis*, and *T. amazonia* trees produced more volume in mixtures than in monocultures. The differences in productivities were most pronounced in *T. amazonia*, *C. brasiliense*, *J. copaia*, and *V. guatemalensis* (Table 5).

4. Discussion

While oftentimes farmers may prefer to plant tree mixtures for aesthetic reasons or to provide habitat for wildlife, in some cases mixtures can also be more productive than fast-growing monocultures (Lamb and Gilmour, 2003; Kanowski et al., 2005). In mixtures, inter-specific competition may be less than intra-specific competition. Moreover, in mixed-species plantations, some species, such as the legumes, may nurse adjacent trees and/or species of trees. Larger tree species can provide needed shelter for more slow-growing species and intercept potential pests. For example, surviving individuals of *Stryphnodendron mycrostachyum* and *Paraserianthes falcataria* were only found in the mixed plots of Plantation 1 and 2, respectively, while all trees of these two species died in monocultures from pest and disease attack as explained in Section 2 (Montagnini et al., 1995; Montagnini and Porras, 1998).

The mixed-species plots in Plantation 1 may also have been more productive than the monocultures because they were able to take advantage of the available growing space, by growing in strata (Lamprecht, 1986; Whyte and Woollons, 1990). In addition, the relatively large increase in volume productions in *J. copaia* and *V. guatemalensis* offset the relatively small reduction in volume seen in the *C. brasiliense* trees, which are disproportionately underrepresented in the plots anyway.

For some species, mixed-species situations can negatively impact productivity. Mixtures may be more heavily stocked than monocultures, and competition for light and water can limit productivity. Competition has nearly extirpated *G. americana* from the mixtures in Plantation 3: only eight trees remain alive in the mixed-species plots. This species is not well adapted to the environmental conditions of the region, for it grows naturally in drier regions (Montagnini et al., 2003). While in monocultures this species can persist, root competition is potentially aggravated by the density of trees found in mixtures.

Light competition also affects productivity. The arrangement of *J. copaia* and *V. guatemalensis* in mixed-species plantations mimics stands with well-spaced crowns. When a 27 m tall *J. copaia* tree is adjacent to a 17 m tall tree, its crown is effectively released on that side. By having shorter *C. brasiliense* trees interspersed amongst *J. copaia* or *V. guatemalensis* trees, essentially these larger trees are closed on fewer sides; and, thus, they will be able to have larger crowns, receive more radiation, be able to fix more carbon, and exhibit faster rates of growth than trees in monocultures (Fry and Poole, 1980; Reukema and Bruce, 1977; Lamprecht, 1986). The opposite is true for the slower-growing tree species such as *C. brasiliense*, which is overtopped by *J. copaia* and *V. guatemalensis* in mixtures. *C. brasiliense* trees did not overtop each other in monocultures: however, their growth was much affected in the mixtures (even if their crowns were closed on all sides). This coincides with earlier findings in these plantations (Montagnini et al., 1995).

Plantations can provide farmers many different environmental services. Mixed-species plantations can often simultaneously provide multiple environmental services as well as provide economic incentives (Lamb and Gilmour, 2003; Kanowski et al., 2005; Montagnini et al., 2005). Monocultures of *V. ferruginea* are used on degraded sites because they produce abundant leaf litter, covering the ground and protecting against soil erosion (Horn and Montagnini, 1999; Stanley and Montagnini, 1999). Mixed plantations showed intermediate levels of soil nutrients in comparison with monocultures (Montagnini and Porras, 1998). Results of other studies in the same experimental setting show that tree regeneration in the understory was more successful in plantations than in abandoned pastures, and that mixed-species plantations demonstrated good results for recuperating understory biodiversity (Carnevale and Montagnini, 2002; Cusack and Montagnini, 2004). Mixed plantations also gave good results in terms of accumulation of above-ground biomass and carbon sequestration (Montagnini and Porras, 1998; Montagnini et al., 2005). As seen in these studies, mixed plantations with native species plantations have social and economic functions, provide forest products, contribute to the rehabilitation of degraded areas, promote atmospheric carbon sequestration, and restore biodiversity.

Acknowledgements

The A.W. Mellon Foundation funded the initial establishment of the experimental plantations at La Selva Biological Station. The Program in Tropical Forestry (Yale University), the Tropical Resources Institute, and the Natural Resources Conservation Service provided funding for the present research.

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